

ARTICLE

Bioenergetics and Trophic Impacts of the Invasive Indo-Pacific Lionfish

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Abstract

Indo-Pacific lionfish, the Red Lionfish *Pterois volitans* and the Devil Firefish *P. miles*, are nonnative marine fish that have invaded the western North Atlantic Ocean, Caribbean Sea, and Gulf of Mexico. Rapid population growth of this invasive predator threatens native fish communities. A bioenergetics model was developed for lionfish (i.e., both species) and then applied to estimate the potential impact of these predators on a reef fish community. We conducted a series of laboratory trials to evaluate consumption and respiration rates between 14°C and 32°C for lionfish weighing from 20 to 400 g. Water temperature greatly influenced consumption; mean daily consumption rates increased from 14°C to 29.7°C and declined at 32.5°C. Energy density of the prey was the most sensitive parameter in the model and estimates of food consumption corresponded with empirical and laboratory estimates. To realize population-level impacts, we applied the bioenergetics model to a size-structured virtual population of 393 lionfish/ha on a reef in the Bahamas. Model simulations estimated that this population would annually consume 929 kg of prey/ha when feeding at 60% of maximum consumption. This model provides the first comprehensive assessment of lionfish bioenergetics accounting for the effects of size and temperature on prey consumption and improves the capacity to evaluate the trophic impacts of lionfish in the Atlantic Ocean.

The Indo-Pacific Red Lionfish *Pterois volitans* and Devil Firefish *P. miles* (together, hereafter referred to as “lionfish”) represent the first successful invasion of nonnative marine carnivorous fishes in the western North Atlantic Ocean

(Meister et al. 2005). Invasive species often undergo rapid population growth in a novel environment (Brown 1989), and lionfish densities have increased dramatically in the invaded range since 2000 (Claydon et al. 2009; Albins and Hixon, in press).

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Lionfish are changing fish community structure on Atlantic and Caribbean reefs (Albins and Hixon 2008; Albins 2013; Green et al. 2012), causing widespread conservation and economic concerns (Elliott and Davison 1975). The ecological impacts of invasive species on native communities can be modeled once the physiological responses and limitations of the invader are well understood (Cooke and Hill 2010). Bioenergetics models provide a useful tool for modeling interactions between predator and prey in many different environments (Hartman and Kitchell 2008). The application of bioenergetics modeling to invasive species has high potential for estimation of impacts, as previously demonstrated by Kitchell's (1990) assessment of Sea Lamprey *Petromyzon marinus* invasion and impacts on native fish communities.

Lionfish were probably introduced into the Atlantic through the aquarium trade (Whitfield et al. 2002; Semmens et al. 2004; Whitfield et al. 2007; Morris and Akins 2009), with the earliest reported sighting in 1985 (Morris and Akins 2009; Morris et al. 2011b). Now established and becoming increasingly abundant, lionfish inhabit both natural and artificial reefs off the southeastern USA, Bermuda, wider Caribbean, and the Gulf of Mexico (Schofield 2009, 2010). Lionfish are commonly observed in habitats ranging from 1 to 300 m. On the U.S. East Coast north of Florida, lionfish are common on deepwater reefs but not in nearshore waters (<35 km from shore) owing to thermal tolerance limits (Kimball et al. 2004). Lionfish are common, however, along shallow coastal reefs and inshore waters of the Bahamas and Caribbean (Green and Côté 2009; Schofield 2009, 2010).

Red Lionfish and Devil Firefish are members of the family Scorpaenidae, subfamily Pteroinae. Both are distinguished in the Atlantic through genetic analysis, Red Lionfish representing 93% of samples collected in 2004 (Hamner et al. 2007). Devil Firefish is native to the Indian Ocean and the Red Sea and previously invaded the Mediterranean Sea via the Suez Canal (Golani and Sonin 1992). Red Lionfish occurs mostly in the Pacific with a range overlap occurring with Devil Firefish in western Indonesia. Mitochondrial DNA analyses by Kochzius et al. (2003) suggested that Red Lionfish and Devil Firefish were indistinguishable as separate species. However, Hamner et al. (2007) and Freshwater et al. (2009a, 2009b) confirmed their separation. In the Atlantic Ocean, morphometric and meristic characteristics overlap, making it difficult to distinguish between the two species (Hamner et al. 2007) without the use of genetics. To date, no differences in reproductive biology have been observed between Devil Firefish and Red Lionfish (Morris et al. 2011b). For this study, we treated the two species collectively because we assume physiological differences between the two species are negligible.

Lionfish populations could have a considerable impact on reef communities by disruption of the food web (Albins and Hixon 2008, in press; Arias-González et al. 2011; Lesser and Slattery 2011; Green et al. 2012; Albins 2013). Lionfish are

generalist piscivores, and most fish and crustacean species common to reef habitats are represented in their diet, including juveniles of the economically important families Serranidae (groupers) and Lutjanidae (snappers) (Morris and Akins 2009). Small juvenile lionfish consume mostly invertebrates, while finfish become increasingly important in the diet through ontogeny (Morris and Akins 2009). Adult lionfish greater than 260 mm TL are almost exclusively piscivorous (>90% by volume), and an individual can consume prey measuring over 50% of its body length (Morris 2009). Predation by lionfish has been shown to reduce recruitment of forage fishes (79% reduction) on experimental patch reefs in the Bahamas (Albins and Hixon 2008) and the biomass of prey fish species (Green et al. 2012). Algae growth levels may be increasing in the mesophotic coral zone due to lionfish consumption of herbivorous fishes, a type of cascading impact that could affect coral biomass (Lesser and Slattery 2011). Direct predation by lionfish may also inhibit the recovery of suppressed stocks of the snapper-grouper complex in the Atlantic Ocean, and lionfish also might compete with adults of these species for space and food (Morris and Whitfield 2009; Albins 2013; Albins and Hixon, in press).

Côté and Maljković (2010) and Green et al. (2011) have empirically quantified prey consumption rates of lionfish using visual census. These studies have shown that light level is influential on lionfish activity, foraging, and predation success with inactivity occurring at night. Peak feeding rates occur during crepuscular periods (Green et al. 2011) and during the day when the weather is overcast (Côté and Maljković 2010). Individual daily consumption rates of lionfish extrapolated from these visual field observations vary greatly and range from 0.038 g of prey per gram of lionfish (Côté and Maljković 2010) to 0.089 g of prey per gram of lionfish (Green et al. 2011). Our approach through bioenergetics modeling expands upon the current knowledge of lionfish prey consumption dynamics through investigating the effect of temperature and body size on consumption. Temperature and body size are controlling factors of fish metabolism and can have profound effects on feeding rate (Elliott and Persson 1978; Boisclair and Sirois 1993).

The Fish Bioenergetics 3.0 model is widely accepted and applied among fisheries biologists (Hartman and Kitchell 2008). This model was initially developed for freshwater fishes in the 1970s and applied to lake systems (Hewett and Johnson 1992). In the decades since, the diversity of applications has expanded to include invasive species such as Sea Lamprey (Kitchell 1990) and zebra mussel *Dreissena polymorpha* (Schneider 1992), and marine fish including Atlantic Cod *Gadus morhua* (Hansson et al. 1996), Yellowfin Tuna *Thunnus albacares*, Kawakawa *Euthynnus affinis*, Skipjack Tuna *Katsuwonus pelamis* (Boggs and Kitchell 1991), and rockfish of the genus *Sebastes* (Harvey 2005). This is one of the first developments and applications of the model to an invasive tropical marine reef fish. Bioenergetics models can account for changing thermal and food conditions

and can be used to evaluate the relative contribution of different factors (e.g., temperature, feeding rate, food availability, food quality).

The goal of this research was to develop a bioenergetics model to estimate the potential predation impacts of lionfish throughout the invaded range. The specific objectives of this study were to (1) develop parameters for a lionfish bioenergetics model through a series of laboratory experiments, (2) calibrate the model via independent growth trials, (3) conduct sensitivity analysis of each model parameter, (4) use the model to estimate field consumption rates as a proportion of the maximum, and (5) estimate total consumption rate of lionfish at densities observed in the Atlantic Ocean.

MODEL DEVELOPMENT

The general bioenergetics model is (Winberg 1960; Hansson et al. 1996; Hanson et al. 1997)

$$C = G + (R + SDA) + (F + U); \quad (1)$$

C = total consumption apportioned to growth,

G = somatic + gonadal growth,

R = metabolism as respiration,

SDA = specific dynamic action,

F = the metabolic cost of digestion as the proportion egested (FA) times the amount consumed,

U = the metabolic cost of waste as the proportion excreted (UA) times the amount consumed.

Somatic growth estimates are typically derived from field measurements and gonadal growth is lost during spawning. In most models, C and R are described by temperature and weight-dependent functions, while the parameters SDA , FA , and UA are constants (Hanson et al. 1997). The equations and subequations are detailed in Table 1.

Consumption.—Scuba divers collected 70 lionfish in 2007 and 2008 approximately 35 km south of Beaufort Inlet, North Carolina, and transported them live to holding tanks and aquaria at the National Oceanic and Atmospheric Administration (NOAA) Center for Coastal Fisheries and Habitat Research in Beaufort, North Carolina. Because lionfish less than 30 g are

TABLE 1. Equations and parameter values (\pm SE) used in lionfish bioenergetics model; all equations from Hanson et al. (1997).

Parameter	Description	Value (SE)
<i>Consumption</i>		
	$C = C_{\max} \cdot p \cdot f(T)_c$ $C_{\max} = CA \cdot W^{CB}$	
CA	Intercept for C_{\max} (g/g per day) at CTO	0.603 (0.1794)
CB	Coefficient of mass dependence	-0.46 (0.0710)
p	Proportion of maximum consumption	0.6
W	Lionfish wet weight (g)	
CQ	Q_{10} value for consumption	4 (0.134)
CTO	Optimum temperature ($^{\circ}C$) for consumption	29.8
CTM	Maximum temperature ($^{\circ}C$) for consumption	34.5
Metabolism		
<i>Respiration</i>		
	$R = RA \cdot W^{RB} \cdot f(T)_r \cdot ACT$	
RA	Oxygen consumption ($g O_2 \cdot g^{-1} \cdot d^{-1}$) by 1 g fish at RTO	0.0085 (0.0014)
RB	Weight-dependent exponent for respiration	-0.28 (0.0484)
RQ	Q_{10} value for respiration	2.33(0.095)
RTO	Optimum temperature ($^{\circ}C$) for respiration	32
RTM	Maximum temperature ($^{\circ}C$) for respiration	34.5
ACT	Activity multiplier	1.8
SDA^a	Specific dynamic action	0.2
Egestion and excretion		
FA^b	Proportion of food consumed egested	0.2
UA	Proportion of food consumed excreted	0.06
Energy density		
<i>Predator</i>	$ED = 2.689W^{0.1545}$	
<i>Prey</i>		4.58
<i>Reproduction</i>	Percent mass released per spawn (female)	1

^aFrom Hanson et al. (1997).

^bFrom Fishelson (1997).

TABLE 2. Water temperature, sample size (*N*), and size range of lionfish used in the consumption trials. Consumption trials were conducted in individual aquaria with fish of different sizes held at constant temperature and fed live prey ad libitum.

Mean (SD) temperature as °C	<i>N</i>	Size range (g)	Length of trial (d)
14.4 (0.6)	12	37–400	15
18.6 (0.5)	9	20–207	9
22.0 (0.7)	12	25–346	8
24.5 (0.8)	4	30–321	7
26.9 (0.7)	21	72–386	8
29.7 (0.6)	10	35–332	6
32.5 (0.6)	12	33–355	8

rarely collected off the coast of North Carolina, an additional 30 small lionfish (1–10 g) were obtained from Quezon Province, Philippines via an aquarium supplier. All lionfish were acclimated to the laboratory at ambient temperature for one month prior to experimentation.

To estimate the allometric parameters for C_{max} (Table 1) we conducted a series of laboratory experiments investigating the dependence of lionfish maximum consumption rate (C_{max}) on temperature and fish size. Maximum consumption was measured in the laboratory at seven temperatures between 14.4°C and 32.5°C using lionfish ranging from 20 to 400 g (Table 2). Kimball et al. (2004) observed cessation of feeding at 13°C; therefore, 14°C was chosen as the minimum temperature treatment. In preliminary trials, lionfish lost equilibrium (became disoriented swimming on its side or upside down) around 34°C, therefore 32.5°C was set as the maximum temperature treatment. Individual lionfish were stocked into 20-L, 40-L, or 110-L glass aquaria (the larger fish were tested in the larger aquaria) in a temperature-controlled water bath connected to a recirculating seawater system with biological and mechanical filtration. System water flowed through each aquarium at a minimum of 10 daily turnovers. Fish were acclimated to the experimental temperature at a maximum of 1°C/d then fed ad libitum for a minimum of 5 d prior to initiating a feeding trial. Live Mummichogs *Fundulus heteroclitus* were collected locally and used as prey. Prey fish ranged from 0.2 to 4.0 g and individuals were <40% of lionfish TL.

To determine total consumption by individual lionfish, the initial mass and number of prey added to each tank was recorded; then the tanks were visually inspected daily and the number of prey consumed was estimated and replaced. At the end of a trial, the mass of unconsumed prey was subtracted from the mass of prey added to the tank. Presence of live prey remaining in the tank at all times after initial feeding indicated that fish were feeding ad libitum (Whitledge et al. 2003). Temperature in the tank was recorded hourly by a digital temperature logger, salinity was 32–36‰, and ammonia and nitrite concentrations remained at <1.0 mg/L. Some fish were tested at multiple temperatures because of the limited availability of lionfish and the

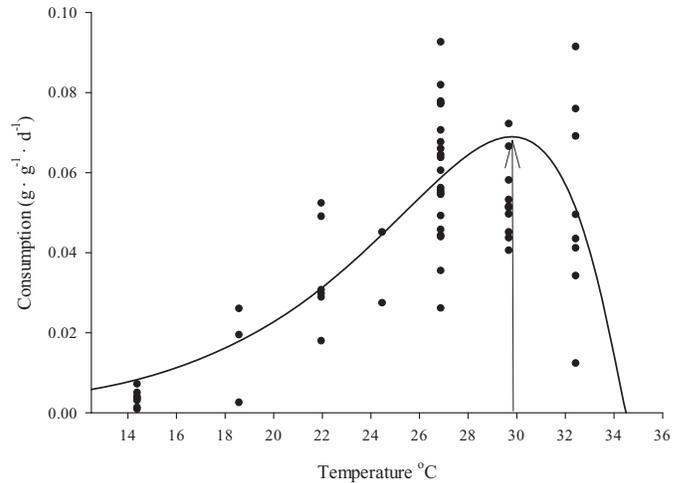


FIGURE 1. Weight-specific consumption rates of lionfish (71–400 g, *n* = 52) as a function of temperature. The curve represents $f(T)_c$, the temperature-dependent function for consumption. The arrow indicates the optimal temperature for consumption, $CTO = 29.8^\circ\text{C}$.

growth that occurred during the study period. No individuals were used more than once at a single temperature or used in consecutive trials.

To determine the weight-dependence of C_{max} we used data from the 10 trials conducted at 29.7°C because this temperature coincided closely with the optimum temperature for consumption, 29.8°C (Table 1; Figure 1). These data were analyzed using nonlinear optimization methods within Solver (Microsoft, Seattle; Microsoft Excel 2012). The sum of squares was minimized to determine the optimum combination of CA and CB values to estimate parameters of the allometric function for C_{max} , (Kitchell et al. 1977; Hanson et al. 1997):

$$C_{max} = CA \cdot W^{CB}, \tag{2}$$

where C_{max} is the specific rate of daily consumption at the optimum temperature (g/g of predator weight), W is body weight (g), and CA and CB are constants (Table 1; Figure 2).

We modeled temperature dependence of consumption using the function $f(T)_c$ equation (2) for warmwater species in Bioenergetics 3.0 (Hanson et al. 1997; Kitchell et al. 1977):

$$f(T)_c = V^X \cdot e^{[x-(1-V)]} \tag{3}$$

$$V = \frac{CTM - T}{CTM - CTO} \tag{4}$$

$$X = \frac{(\ln(CQ) \cdot (CTM - CTO))^2 \cdot \frac{[1+(1+40)^{0.5}]^2}{\ln(CQ) \cdot (CTM - CTO + 2)}}{400} \tag{5}$$

We set CTM (maximum temperature for consumption) to 34.5°C because we observed lionfish mortality at this temperature, and it is within the range of lethal maxima reported for tropical marine fishes (Menasveta 1981). Values for CQ (Q_{10} , or rate of increase over relatively low temperatures) and CTO (optimum

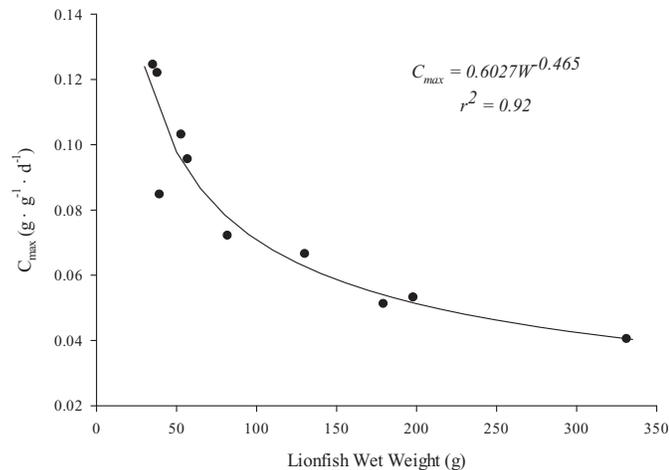


FIGURE 2. Allometric maximum consumption rates ($y = 0.603x^{-0.465}$, $r^2 = 0.924$) of lionfish ($n = 10$) from laboratory experiments at 29.7°C.

temperature for consumption) were estimated using consumption rates from the individual consumption trials conducted with lionfish ranging from 20 to 400 g, fed ad libitum at temperatures from 14.4°C to 32.5°C. We fit the function $f(T)_c$ to these data using the nonlinear optimization methods within Solver (Microsoft Excel 2012). The sums of squares were minimized to determine the optimum combination of CQ and CTO values (Table 1).

Respiration.—Using automated intermittent flow respirometers, resting metabolic respiration rates of 23 lionfish from 20 to 331 g were measured at three temperature means (SD): 5 fish at 17.5°C (0.4), 7 fish at 23.3°C (0.9), and 11 fish at 29.1°C (0.4). Small fish (≤ 100 g) were placed in a gasket-sealed 4.3-L acrylic tube, and larger fish in a rectangular 40-L glass aquarium with a sealed lid. Systems were submerged in a temperature-controlled water bath. Water was pumped into respirometers from an aerated reservoir containing seawater that had passed through a 5- μ m paper cartridge filter and ultraviolet sterilizer to minimize microbial respiration. Two trials at each temperature were run with no fish in the chamber to assess background microbial consumption of oxygen; none was detectable. The recirculating pump ran continuously, and the flush pump ran intermittently (timer controlled) to supply the system with oxygenated water. Gentle flow through the chambers at 0.1–0.3 cm/s allowed the fish to be in a resting state. An automated data logger attached to a galvanic dissolved oxygen (DO) probe (WTW Oxi 3400i) recorded DO concentrations at intervals of 60 s or less throughout each trial. Between flushes, the system was closed and the observed rate of decline in DO was used to calculate specific rate of respiration. An oxycaloric conversion factor (0.014 kJ/mg of O_2 consumed) was used to convert oxygen consumed to kilojoules (Elliott and Davison 1975). The length of interval between flushes was adjusted to maintain minimum DO levels above 5 mg/L. After the fish had acclimated to the chamber for at least 2 h, a minimum of five cycles was recorded for each fish.

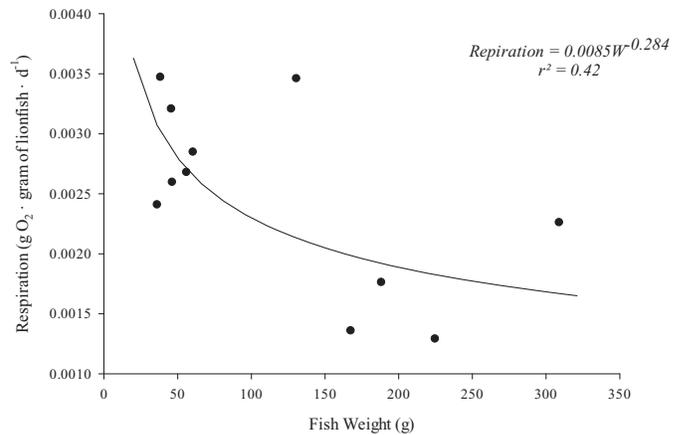


FIGURE 3. Allometric resting metabolic rate (grams of O_2 per gram of lionfish per day) of lionfish (36–309 g; $n = 11$) at 29.1°C.

Respiration was modeled as

$$R = (RA \cdot W^{RB}) \cdot f(T)_r, \quad (6)$$

where RA and RB are allometrically fit parameters (Figure 3). Parameter estimates for the respiration temperature function $f(T)$ followed the same form as consumption, except CTM , CTO , and CQ are replaced by RTM , RTO , and RQ (Q_{10} , or rate of increase over relatively low temperatures). The thermal maximum (RTM), was set at 34.5°C. We fitted the function $f(T)_r$ to these data using the nonlinear optimization methods within Solver (Microsoft Excel 2012). The sum of squares was minimized to determine the optimum combination of RQ and RTO values (Table 1).

Excretion, egestion, and specific dynamic action.—The proportion of consumed energy excreted (UA) was measured as total ammonia nitrogen (TAN) for nine individual lionfish (4–15 g) at 27°C. Fish were placed in 10-L containers with flow-through ammonia-free seawater. Each fish was fed grass shrimp *Palaemonetes spp.* to satiation (2–5 prey items), and the mass consumed was recorded. The TAN concentration was measured hourly for 12 h until the concentration was zero. The TAN concentration for each hour interval was multiplied by the flow rate, and the total mass of ammonia nitrogen was calculated for the entire period. This mass was converted to energy using the oxycaloric coefficient of 24.9 kJ/g (Elliott and Davison 1975). The energy density of grass shrimp was reported by Anderson (1974) and de la Cruz (1983) as 18.42 kJ/g dry weight (W_{dry}). Grass shrimp wet weights were converted to dry weights using the equation:

$$W_{dry} = 0.245y + 0.5, \quad (7)$$

where y is individual wet weight (g; Anderson 1974). For each fish tested the amount of energy excreted as ammonia nitrogen

was divided by the amount of energy consumed, and the results were averaged to estimate UA ($UA = 0.06$, $SD = 0.04$; Table 1).

The proportion of energy egested (FA) was calculated based on fecal production reported by Fishelson (1997), where the reported range of masses of dried feces produced by lionfish fed known meal sizes (40–80 g) of live tilapia *Oreochromis spp.* yielded 1.03–3.03 g dry feces and meals consisting of 20–24 g of Western Mosquitofish *Gambusia affinis* yielded 0.92–1.45 g dry feces. The prey fish wet weights were converted to dry weights using

$$W_{dry} = 0.24 W_{wet}, \quad (8)$$

where W_{dry} (g) is whole fish dry weight and W_{wet} is whole fish wet weight. This equation is based on the reported moisture content for tilapia (Wang et al. 2002; Badwy et al. 2008) and closely matches the moisture content of Mummichogs measured in this study. The proportion of mass remaining as feces was calculated for the minimum and maximum consumption reported by Fishelson (1997), and the mean of those values is reported as $FA = 0.20$ (SD , 0.06; Table 1). Our estimates for UA , FA , and SDA are similar to those used in bioenergetics models of other carnivorous fishes (Rice et al. 1983; Hanson et al. 1997). The metabolic cost of digestion, SDA , typically ranges between 0.15 and 0.2 (Hanson et al. 1997). High protein diets of carnivores require more digestive energy (Tytler and Calow 1985), so we chose 0.2 for SDA in the lionfish model.

Energy density.—Gross energy content of 27 lionfish (51.6–458.9 g) was measured by proximate chemical composition analysis on whole body samples of lionfish collected off the coast of North Carolina. Proximate analysis was also performed on 17 lionfish egg masses collected in the laboratory and 25 whole Mummichogs that were used as prey in feeding trials. Samples were freeze-dried, homogenized, and lipids were extracted using a Soxhlet apparatus with petroleum ether solvent (Dobush et al. 1985). Ash content was determined by burning off all remaining organic content at 450°C for 12 h in a muffle furnace. Carbohydrate content of fish is assumed to be zero (Henken et al. 1986). The protein content was calculated by subtracting the percent fat and ash from 100%. Proportional dry matter compositions were multiplied by caloric values of 0.0396 kJ/g for fat and 0.0237 kJ/g for protein (Henken et al. 1986) and summed. This method provides results equivalent to combustion in a bomb calorimeter (Henken et al. 1986). The energy density of lionfish increased with body size (Figure 4). Lionfish energy density (ED ; KJ/g) can be inferred from percent dry weight ($100 \cdot \text{dry weight/wet weight}$; Figure 4A) or total wet weight of an individual (Figure 4B). The energy density curve profiles were fit using SigmaPlot version 12.0, from Systat Software, Inc., San Jose, California.

Model calibration and determination of activity.—Fish metabolism increases with activity level. In the bioenergetics model this is accounted for by the activity multiplier, ACT . Thirteen lionfish ranging from 121 to 693 g were held in 100-L tanks and fed 0.10–0.35 g/d of live prey per gram of predator

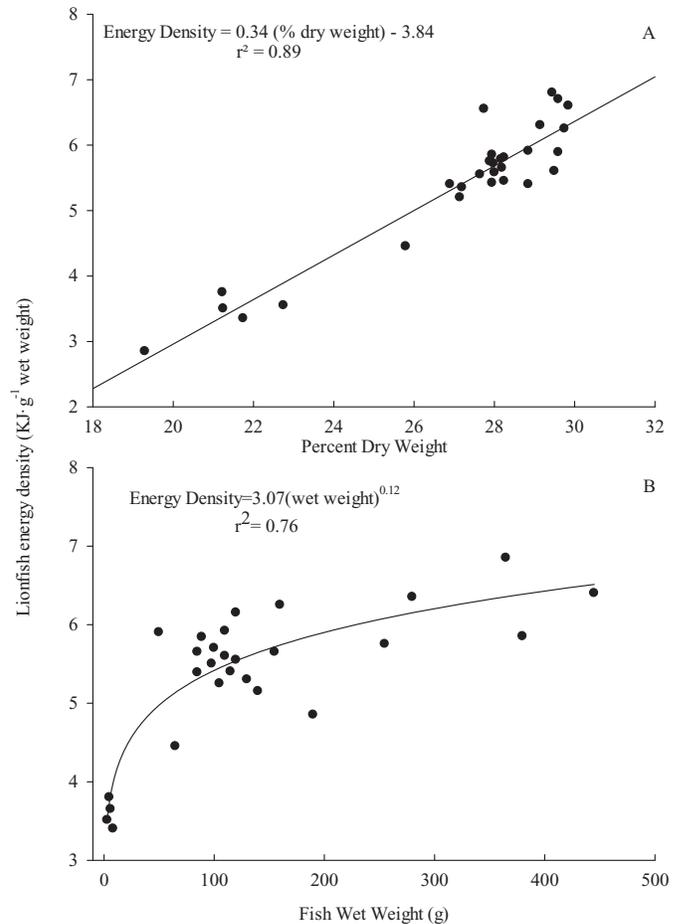


FIGURE 4. (A) Lionfish ($n = 29$) energy density as a function of percent dry weight, i.e., 100 (dry weight/wet weight). (B) Relationship between fish wet weight and energy density ($n = 29$).

weight for 19 or 20 d. The mass of each individual lionfish was determined at the beginning and end of the growth trial. Total mass of prey consumed was also determined at the end of each trial. Water temperatures were recorded daily and mean temperature for the trials ranged from 21°C to 28°C. The results of these trials were used to calibrate the model by entering growth and daily temperature values and iteratively adjusting ACT to minimize the percent of error between predicted consumption and observed consumption from these 13 trials. The resulting value for ACT was 1.8, which is within the range of commonly used values for relatively inactive fish (Tytler and Calow 1985).

To corroborate the lionfish model and the final parameter values, additional feeding trials were conducted using the same experimental methods as for the activity trials. The observed prey consumption from each trial was compared to the predicted consumption model using our final model parameters. The predicted consumption estimates fit well with the observed consumption (Figure 5). The mean difference between predicted and observed consumption was -5.4% (SD , 2.1). Over 61% of the model predictions differed 15.0% or less from observed

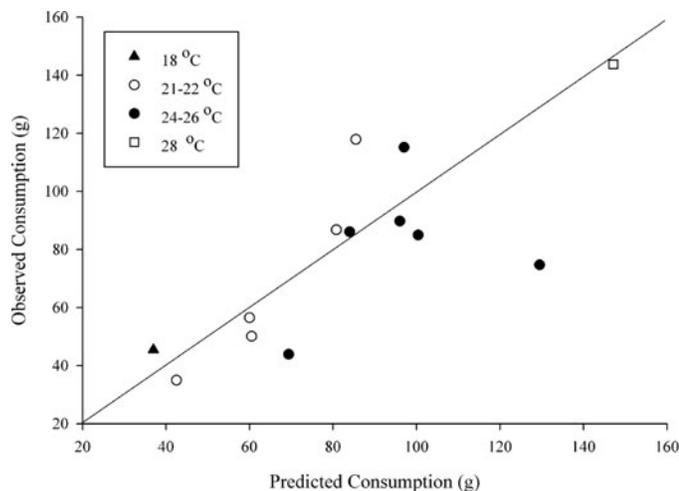


FIGURE 5. Performance of model where each point represents the model-predicted consumption based on observed growth versus the actual consumption observed during 19–20-d laboratory trials. The line signifies a 1:1 relationship.

consumption, and the remaining predictions were within 40% of observed consumption for the recorded trials.

Sensitivity analysis.—A sensitivity analysis was conducted to identify the relative influence of each parameter on model output. One individual growth trial was selected, representing a median lionfish size and feeding ration. Each model parameter (Table 1) was adjusted $\pm 10\%$, except temperatures, which were adjusted by $\pm 1^\circ\text{C}$ (after Kitchell et al. (1977)). The predicted mass of prey consumed was recorded for each model run, and the mean percent change in consumption was calculated for each parameter. Overall, the lionfish model exhibited low sensitivity to 10% perturbations in individual parameter estimates. A 10% reduction in prey energy density was the only alteration that resulted in more than a 10% change in prey consumption (+11.6%). Adjusting respiration model parameters changed the predicted consumption less than 6%. All of the consumption parameters exhibited low sensitivity, with the results changing less than 1% (Figure 6).

The sensitivity of consumption rates was modeled by simulating consumption at different temperatures (22–35°C) and ration levels (P), ranging from 0.0 to 1.0 as a proportion of maximum consumption (C_{\max}). The daily consumption by juvenile (5.0 g), subadult (35.0 g), and adult (148.0 and 340 g) lionfish was estimated and summed for a 365-d period to estimate annual consumption. Consumption rates increased with ration for all sizes of fish. Consumption rates increased with temperature to 30°C and decreased at 32°C (Figure 7). The P -values for maintenance ration (amount of food consumed to achieve zero growth) ranged from 0.2 to 0.38 for juvenile and subadult fish and from 0.33 to 0.53 for adults. A juvenile lionfish (5.0 g) could consume 1,305 g of prey at 22°C and over 7,310 g of prey at 28°C feeding at its maximum ration ($P = 1.0$, C_{\max}). This consumption rate pattern was consistent for all other sizes (Figure 7).

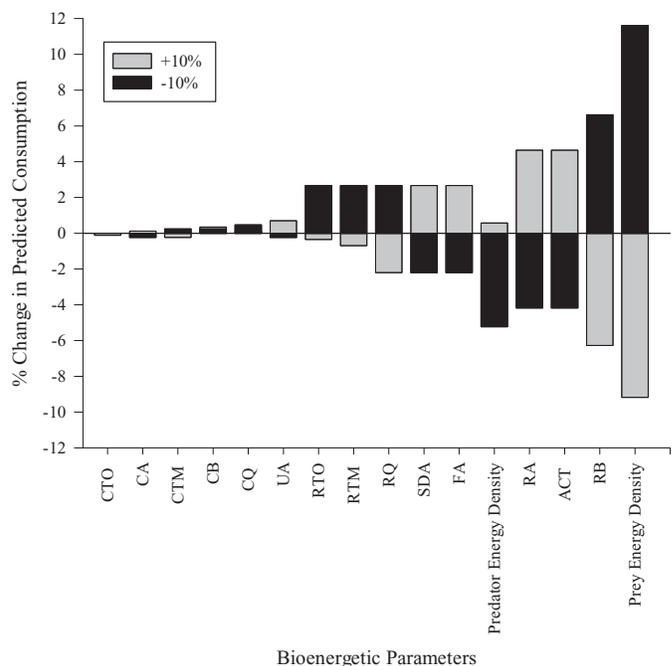


FIGURE 6. Sensitivity of lionfish bioenergetics model consumption estimates to changes in each model parameter. The baseline simulation predicted consumption of 86.1 g of prey by a lionfish that grew from 146.6 g to 168.7 g during a 19-d growth trial at a mean temperature of 24.8°C (actual consumption = 84.5 g of Mummichogs). In individual model runs each model parameter was increased or decreased 10%, except temperatures, which were increased or decreased 1°C. Bars indicate the percent change in predicted consumption when the parameter value was increased (grey bars) or decreased (black bars). See Table 1 for bioenergetics model parameter descriptions.

MODEL APPLICATION

To demonstrate an application of the bioenergetics model, we simulated annual consumption of a lionfish population on a patch reef off the coast of New Providence, Bahamas with an assumed size distribution based on length-frequency data from 586 lionfish collected in the Bahamas in 2008 (Figure 8; J. Morris and L. Akins, unpublished data). This required that we first determine an appropriate value of P , the proportion of maximum consumption, to use in these simulations. We obtained estimates of annual lionfish growth in the wild for eight age groups (1–8 years) using a Von-Bertalanffy growth function developed from otolith analysis of 134 individuals from North Carolina (J. Potts, National Marine Fisheries Service, unpublished data). While annual increments have not yet been validated for this species, the curve provides an estimate of annual growth by the population. We used these estimates of annual growth in the lionfish bioenergetics model, along with mean sea surface temperatures for each month from offshore North Carolina (NO-MADS, Rutledge et al. 2006) and a constant prey energy density of 4,580 J/g wet weight in the simulations. The mean P -value from the eight simulations was 0.6 (SD, 0.06).

The diet composition was held constant (prey energy density of 4,580 J/g wet weight) for all simulations, and individual growth and consumption were simulated over a 1-year period.

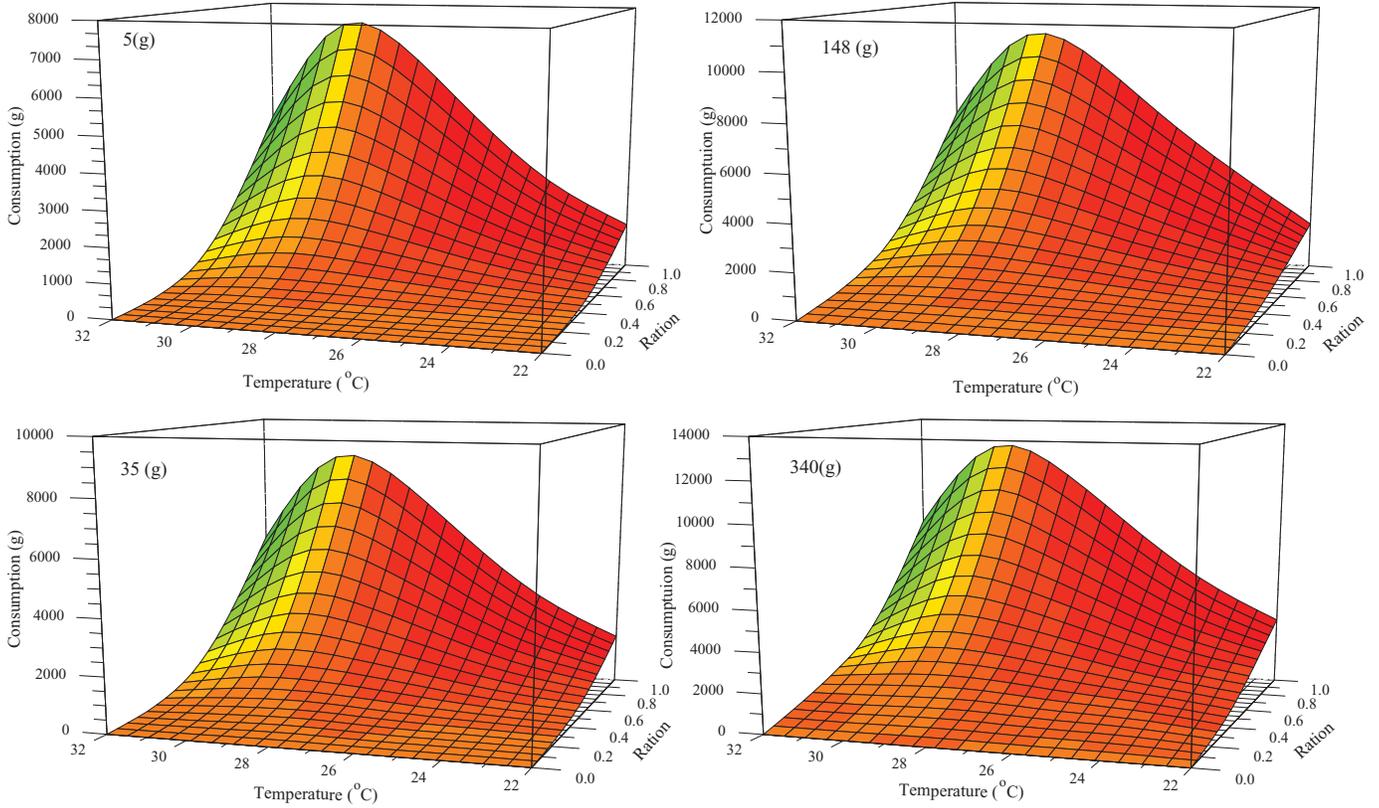


FIGURE 7. Simulated cumulative annual food consumption as a function of ration (0.0–1.0 maximum consumption) and temperature (22–32°C) for juvenile (start size, 5 g), subadult (start size, 35 g), and adult (start sizes, 146 and 340 g) lionfish from 365-d bioenergetics model simulations. To approximate daily consumption (grams of prey per gram of lionfish), the annual consumption was divided by 365 d and the weight of the fish. [Figure available online in color.]

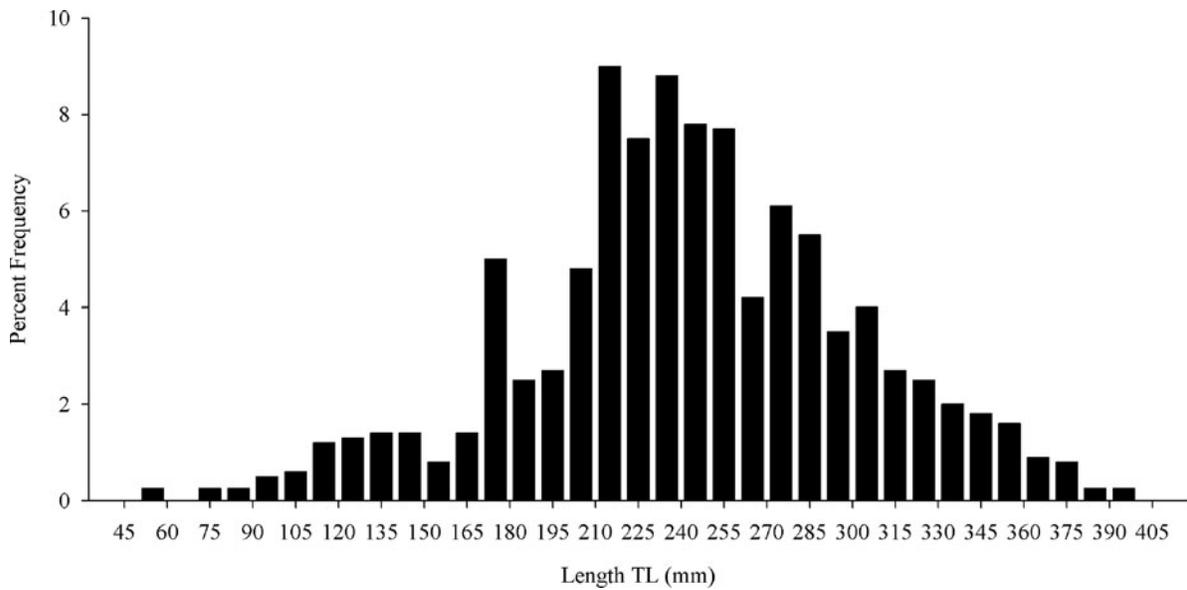


FIGURE 8. Size frequency distribution of 586 lionfish collected in the Bahamas in 2008 (J. Morris and L. Akins, unpublished data). This size distribution was used to structure the population-level consumption via a bioenergetics model (see Table 3).

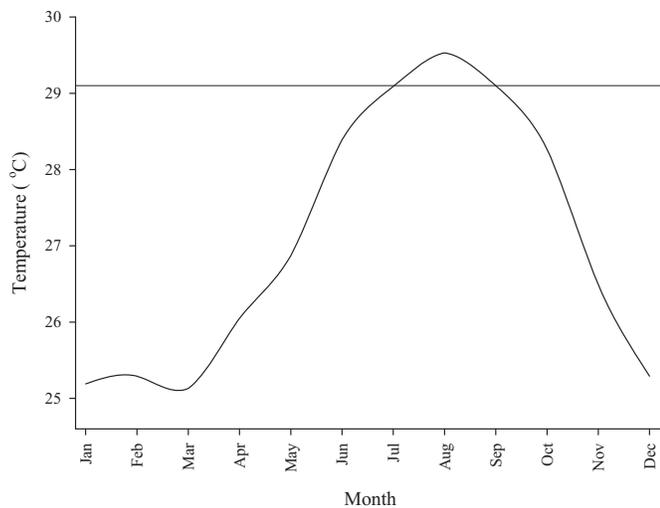


FIGURE 9. Average monthly sea surface temperatures (SST; NOMADS) in 2008 from New Providence, Bahamas ($25^{\circ}04.6'N$, $77^{\circ}20.6'W$). Line represents $29.1^{\circ}C$, the optimum temperature for lionfish consumption.

The temperature input data consisted of sea surface temperatures, SST (NOMADS; Rutledge et al. 2006) from New Providence, Bahamas (Figure 9). Individual consumption was scaled to the population level using density estimates from Green and Côté (2009), who reported a density of 393 lionfish/ha on Bahamian reefs. We structured our population consumption estimates by multiplying the proportion of fish in each size-class by the total number lionfish per hectare (Table 3). We applied a constant annual mortality rate of 0.052 for size-class 1 (SC1) and 0.165 for the remaining size groups (Morris et al. 2011a).

The SST data showed a typical profile for tropical areas: a general warming pattern through the spring and a decline in water temperature through the fall (Figure 9). From June through September, the water temperatures were near the optimal temperature ($29.1^{\circ}C$) for lionfish consumption. Individual fish in SC1 consumed 1,246 g of food annually and gained 333 g of biomass (Figure 10A). The SC4 fish consumed 3.1 times more food (3,956 g) over the course of a year than fish in the SC1 group (Figure 10A). Annual consumption by the entire population was estimated at 929 kg/ha. The SC2 and SC3 groups were

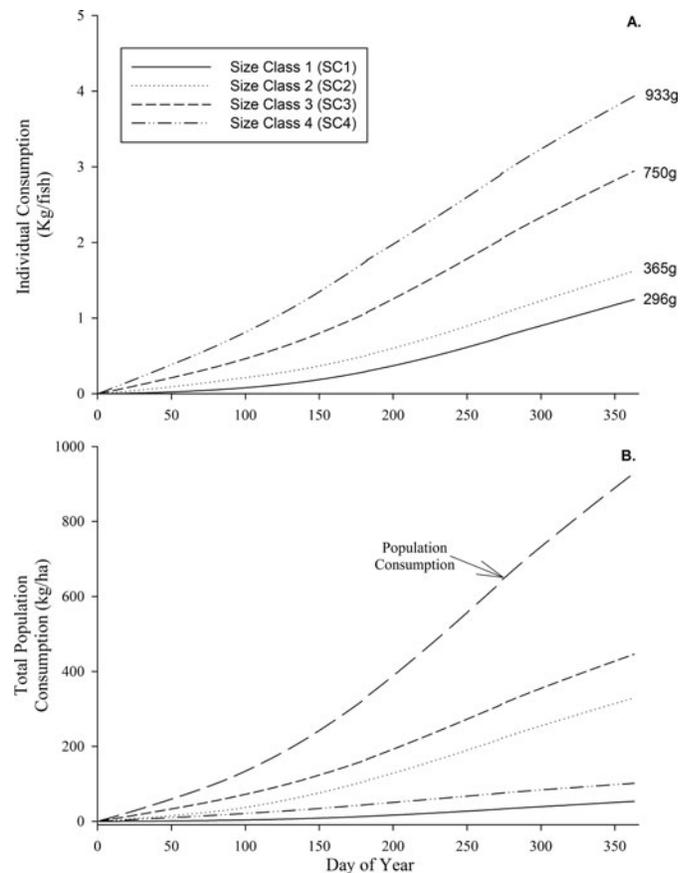


FIGURE 10. Cumulative consumption by an individual fish (A) in each size-group, and (B) by all fish in each size-group and the total population, as estimated using the bioenergetics model for lionfish on a coral reef off New Providence, Bahamas. The numbers to the right of each line in panel (A) indicate the final weight of individual fish in each size-group at the end of the simulation (day 365).

responsible for 83% of the population-level consumption: 35% for SC2 and 48% for SC3. The SC1 and SC4 groups collectively accounted for 17% of the consumption (Figure 10). The SC2 and SC3 groups consumed most of the biomass because these groups collectively made up 81% of the individuals in the population (Table 3).

TABLE 3. Model inputs and life table parameters for lionfish off the coast of the Bahamas. Except where indicated otherwise, all values were gathered from unpublished data or personal communication. Lengths were converted to weights using a relationship determined from pooled collections of 782 individuals from North Carolina and the Bahamas ($W = 0.000002285L^{3.335}$, $r^2 = 0.97$). Values are for day 1 of the 1-year simulations. The percent of the population and initial population size are based on the size frequency distribution of a lionfish population on a reef off the coast of Bahamas with a density estimate of 393 lionfish/ha. The annual mortality rates are from Morris et al. (2011a).

Size-class	Start length (TL; mm)	Start weight (g)	Percent of the population	Initial population size (number/ha)	Mortality
SC1	50	1.05	12.2	48	0.165
SC2	145	37.0	41.6	173	0.052
SC3	235	184.0	39.6	146	0.052
SC4	325	544.0	6.6	26	0.052

DISCUSSION

To our knowledge, this is the first complete bioenergetics model for a tropical marine reef fish developed from laboratory-derived parameter estimates. Strong agreement between the calibrated model's predictions of prey consumption and observed rates in the laboratory trials invoke further confidence that this lionfish model accurately predicts consumption. Lionfish consumption may cause significant impacts on food web dynamics of reef ecosystems (Morris and Akins 2009; Green et al. 2011; Lesser and Slattery 2011; Albins and Hixon, in press). As expected, the observed temperature-dependence of consumption rate indicates that predation rate will vary seasonally and latitudinally across the lionfish's invasive range.

There are two published empirical studies that provide field estimates of specific daily consumption for lionfish (Côté and Maljković 2010, Green et al. 2011) and one laboratory estimate (Fishelson 1997). Côté and Maljković (2010) used underwater visual field observations and estimated daily consumption at 0.038 g/g of a 340 g lionfish feeding at 23°C. Our model predictions suggest that Côté and Maljković's (2010) estimate is equivalent to a 340-g fish feeding at maximum consumption ($P = 1.05$) at 23°C. From visual observations in the Bahamas, Green et al. (2011) estimated specific daily consumption of 0.089 g/g for a 148-g lionfish at 26°C. Using our model, this estimate is equivalent to a 148-g lionfish at 26°C feeding at 84% of maximum consumption ($P = 0.84$; Figure 7). Fishelson's (1997) daily consumption estimate for a 350-g lionfish was approximately 0.024 g/g of lionfish at temperatures between 23°C and 24°C. Our model indicates that this feeding rate represents 78% of its maximum consumption ($P = 0.78$). The daily consumption estimates from Fishelson (1997), Côté and Maljković (2010), and Green et al. (2011) are all possible based on our model, but all represent high feeding rates ($P > 0.75$) not typically observed in the field for most fishes. While juvenile fish sometimes feed to satiation ($P = 1.0$) in the field (Persson et al. 2000; Feeney et al. 2012), feeding rates of adult fish in the wild are typically between 30% and 50% ($P = 0.30$ – 0.50) of their maximum consumption (Rice and Cochran 1984; Beauchamp et al. 1989; Kitchell et al. 1994; Hartman and Brandt 1995).

Several factors may account for the differences in daily consumption estimates among these studies. Green et al. (2011) noted that their daily consumption estimates were about three times higher than reported by Fishelson (1997) and Côté and Maljković (2010). These direct comparisons should only be made if the consumption estimate is adjusted for the effect of temperature. For example, a 148-g lionfish feeding at 28°C will consume 2.2 times more food than at 24°C (Figure 7). Green et al. (2011) and Côté and Maljković (2010) estimated daily consumption of lionfish in the field based on underwater visual estimates of lionfish lengths and lengths of the prey consumed. Visually estimated lengths were then converted to estimated weights using a weight-length relationship from Froese and Pauly (2000), where weight increased as approximately the cube

of length. Thus, small errors in length estimates will be further compounded in the conversion to weight. It is well demonstrated that underwater visual estimates of fish length are prone to significant error and high variability (Bell et al. 1985; Harvey et al. 2002; Harvey et al. 2004). This type of error in estimated fish size may have contributed to the high variability in lionfish prey size reported by Green et al. (2011), which was more than 100% of the mean, 1.47 g (SD, 1.58). Further, the use of consumption rate of an average lionfish at a single temperature can lead to errors if extrapolated to populations over time. We have demonstrated the strong influence of temperature and body size on consumption rates (Figures 1, 2 and 7).

The differences in the annual consumption among the four size groups of lionfish we modeled were because of a combination of differences in initial sizes at the start of the simulation (day 1) and the size structure of the population. Size groups SC2 and SC3 represented over 80% of the individuals in the population and accounted for 83% of the prey consumed by the population. Our simulated lionfish population consumed 0.93 metric tons of prey/ha per year. Because we modeled a population experiencing only natural mortality and no recruitment or settlement to the reef, this estimate is likely an underestimate of consumption.

The strength of our modeling effort is that we built the lionfish model by directly measuring temperature-dependent and weight-dependent specific rates of nearly all components of the energy budget. Direct measurement of these parameters in the laboratory minimizes error that can arise from using assumed parameters in a bioenergetics model (Ney 1993). Although some studies have evaluated the metabolism of warmwater marine reef fish juveniles (Wuenschel et al. 2005) and adults (Claireaux and Lagardère 1999; Kline 2004), using estimates from these studies was not appropriate because lionfish have several characteristics that differ from typical reef fish, such as venom defense, large pectoral fins, slow swimming speed, and skin sloughing (Fishelson 1997). Because of the uncertainty associated with the energetic demands of these characteristics, all model parameters were directly obtained from laboratory experiments except for egestion and SDA, which have low variability from species to species and are difficult to measure in the laboratory (Hanson et al. 1997). This has contributed to the robustness, stability, and reliability of this model.

The juvenile and adult life stages of some fish species have different allometric curves for metabolism (Post 1990). We developed a single-stage bioenergetics model and did not develop a separate model for adults and juvenile lionfish because juvenile lionfish are difficult to obtain from the field and in the laboratory can quickly grow to adult sizes. We are able to account for the dietary shift that occurs during lionfish ontogeny. This approach may be refined in the future if future studies provide estimates of juvenile lionfish metabolism that are different from adults. The application of the single-stage bioenergetics model to our reef population of lionfish is appropriate, however, because only 6%

of the population observed in field collections were juveniles (<30 g; Figure 8).

The activity multiplier (ACT) we estimated for lionfish (1.8) is similar to the ACT estimated for Southern Flounder *Paralichthys lethostigma* (2.1), another low-activity piscivore (Burke and Rice 2002). Activity can be a significant source of error when using bioenergetic models to estimate total consumption of fish populations (Ney 1993), and lionfish devote considerable time to hovering or hiding (Fishelson 1997). The activity level of lionfish in the Atlantic compared with the Indo-Pacific is unknown. While lionfish are commonly found resting during the day and have elevated activity levels during crepuscular periods, Green et al. (2011) and Côté and Maljković (2010) reported that some lionfish in the Bahamas were actively feeding during the day; thus, activity levels are likely to vary across habitats, time of day, weather conditions, water current velocities, and prey densities.

Fishelson (1997) reported laboratory-measured consumption and growth rates of individual Red Lionfish (Devil Firefish; see Hamner et al. 2007) that differ from the predictions of this bioenergetics model. Using the temperature, prey type, and growth data from Fishelson (1997) resulted in considerably lower consumption estimates from the bioenergetics model than were observed. Adjusting the activity multiplier (ACT) to greater than 5.0 was required to predict consumption similar to that reported by Fishelson (1997), but this is unrealistically high for the activity level observed for lionfish. Additionally, when the ACT was elevated, the model's sensitivity increased considerably. The differences in growth between the two studies may be attributed to (1) varied duration of growth periods (Fishelson 1997 reported growth intervals of 1–14 months versus 19–20 d in this study), (2) geographical or genetic differences between the lionfish leading to differences in energy budgets, and (3) laboratory holding conditions such as tank size, prey type, feeding schedule, and habitat availability (Fishelson provided structure in the tank, but we did not). Growth and consumption rates were variable among the size-classes in that study and did not show expected trends of size dependence. We attempted to reevaluate the data collected in Fishelson's study, but unfortunately the records were lost during a fire (L. Fishelson, personal communication).

The sensitivity analysis used to evaluate this lionfish bioenergetics model is a standard method that has been employed in numerous bioenergetics studies (e.g., Kitchell et al. 1977). The analysis shows that the sensitivity of each individual parameter was low, possibly because of low resting metabolic rates and high consumption rates. Prey energy density and respiration model parameters exhibited the highest sensitivity to error. The respiration parameters are typically most sensitive in bioenergetics models and prey energy density is generally one of the least sensitive parameters (Rice et al. 1983). The energy density of prey used in this study was measured and found to exhibit low variability. The same prey energy density was also used during model simulations of lionfish in reef habitats because estimated energy content for species common in lionfish diet

was unavailable in the published literature. Deriving the majority of parameters from direct laboratory measurement probably improved the robustness of model performance.

This work demonstrates the magnitude of predatory demand that invasive lionfish are now imposing on Atlantic reef communities. Alarming, lionfish at high densities can consume a significant proportion of the standing stock biomass of reef communities. In marine protected areas, there are typically 1,000–1,500 kg of prey fish of various species per hectare of coral reef (McClanahan et al. 2011). Our modeled size-structured virtual population of 393 lionfish/ha consumed 929 kg of prey per hectare annually. The influence that this magnitude of consumption will have on community structure and food web dynamics represents an abrupt change to the reef community and warrants further investigation. High resolution measurements of replenishment rates or turnover of prey fish biomass within these systems are needed to elucidate the relative scale of lionfish consumption and its impact on biodiversity of reef fish communities. Additionally, estimates of in situ growth of lionfish in different habitats, coupled with estimates of local prey abundance, will allow for site-specific and seasonal estimates of the feeding rate of lionfish populations. These estimates can be obtained through mark–recapture studies and otolith increment analysis. Further measurement of the energy content of common reef fish species will also improve model performance because prey energy density was the most sensitive parameter.

The low sensitivity of parameters and strong agreement of model predictions with laboratory growth data indicate that the model presented here provides a relatively accurate depiction of lionfish energetics. Future research can enhance this modeling framework to further calibrate for specific locations and hone the ability to quantify lionfish impacts on reef communities and fisheries. Model simulations can help develop and evaluate removal strategies to mitigate impacts, the scale of which is likely to increase rapidly as this unprecedented invasion progresses both spatially and temporally. This bioenergetics model can also be integrated with research on community interactions and individual species to quantify the influence of lionfish consumption on community structure and food web dynamics. The energetic parameters developed here can be incorporated into network models developed for marine reef ecosystems (Opitz 1993; Deehr et al. 2007). Many studies have characterized reef community structure (e.g., Harborne et al. 2008) and recruitment (e.g., Tolimieri et al. 1998), and observed patterns could change as lionfish alter energy flow within these food webs in their newly settled areas.

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